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Advertisement call structure and morphology of *Breviceps mossambicus* Peters and *B. poweri* Parker (Anura: Microhylidae) from northern Mozambique

by

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ABSTRACT

An analysis of advertisement calls indicates that a population of *B. mossambicus* from the type locality, Mozambique Island, and two populations from the adjacent mainland, are conspecific. *B. mossambicus* calls differ from those of *B. adspersus* from Pietersburg, South Africa, with regard to call duration, number of pulses and the grouping of calls within the call bout. These differences support the recognition of *adspersus* and *mossambicus* as separate species.The calls of *B. poweri* from Nampula are unpulsed and are grouped within the call bout to a greater extent than those of *mossambicus* and *adspersus*. Certain morphological characters are examined and their diagnostic value is discussed.

INTRODUCTION

Peters' 1854 and 1882 descriptions and illustration of *Breviceps mossambicus* appear to be based on specimens from Mozambique Island. However, he also referred specimens from a mainland locality, Sena, about 665 km to the southwest, to this species; this material seems to be lost (Poynton & Broadley 1985). Mainland material referred to *mossambicus* by Poynton (1964 1966), Poynton & Broadley (1985) and Lambiris (1989) is darker dorsally and generally lacks the dark spots and light vertebral stripe possessed by most Island specimens.

Identification of mainland material is complicated by the fact that some specimens possess markings intermediate between those presently considered to be diagnostic for *B. mossambicus* and *B. adspersus*. Poynton (1966 1982), Poynton & Broadley (1985) and Lambiris (1989) regard this as evidence of extensive hybridisation between these species where their ranges overlap. Broadley (1966 1971), Pienaar *et al.* (1976) and Poynton (1980) even considered *adspersus* to be a subspecies of *mossambicus*. Further investigation was therefore necessary to clarify the relationship between these two taxa.

The advertisement call in frogs is a character of great diagnostic value at species level (Poynton 1964: 5; Passmore 1981 1985; Minter 1995, for additional references). This study describes the advertisement call structure of *B. poweri* at Nampula, and of Island and mainland populations of *B. mossambicus* and compares their calls to those of *B. adspersus* from Pietersburg, South Africa, described elsewhere (Minter 1995).

LOCALITIES, SAMPLING METHODS AND DATA ANALYSIS

Collection of specimens and recording of their advertisement calls

a) *B. mossambicus* and *B. poweri* were collected on 28–29th November 1994, in a cashew plantation 5 km east of Nampula, just north of the road to Mozambique Island; 15°06'S 39°20'E; altitude 450 m; about 160 km from the coast. The undergrowth beneath the trees had been cleared and the leaf-litter raked into piles, leaving the ground fairly bare. The soil was a grey, sandy loam, damp from recent rain. The calls of 20 *mossambicus* and 40 *poweri* individuals were recorded, and 21 male *mossambicus* and 40 male and one female *poweri* specimens were collected and preserved (one *poweri* specimen frozen for electrophoresis), including an amplexing pair of the latter species.

b) *B. mossambicus* was collected on 1st December 1994, calling from undergrowth and thick leaf-litter beneath a small copse of trees in grassy, short, closed woodland next to the road between Nampula and Mozambique Island, approximately 20km west of Lumbo, a settlement on the coast adjacent to Mozambique Island; 14°59'S 40°30'E; altitude 100 m. The soil was a grey, sandy loam, damp from recent rain. Calls of 5 individuals were recorded and 6 males were collected and preserved (one frozen for electrophoresis).

c) *B. mossambicus* was collected between 30th November and 7th December 1994, in a public park on Mozambique Island; 15°02'S 40°44'E; altitude 5 m. The light-brown, sandy soil had a sparse covering of grass in the open areas and a thick covering of leaf-litter beneath broad-leafed *Ficus* trees on the perimeter of the park. The soil was damp from recent rain. Calls of 58 specimens were recorded, 34 were weighed and released, and 18 male and 3 female specimens were collected and preserved (one male frozen for electrophoresis).

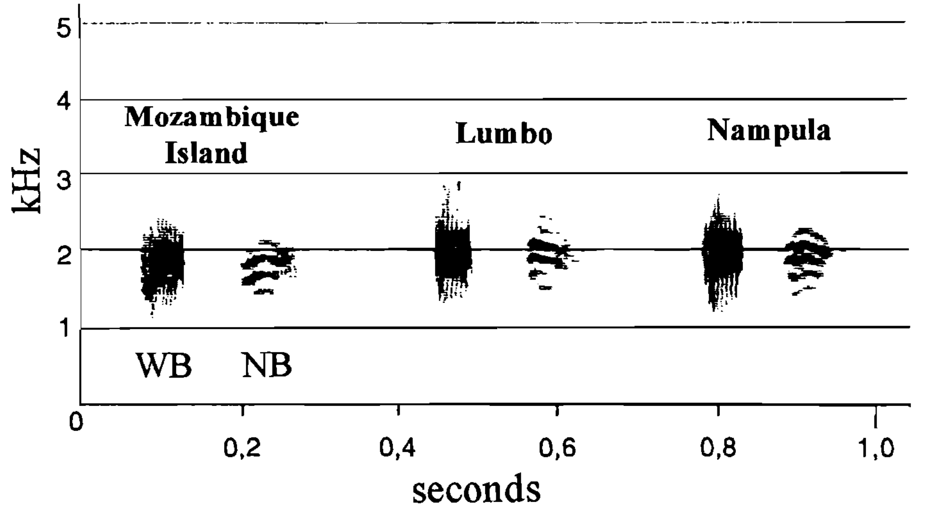

Fig. 1. Wide (WB) and narrow band (NB) sonagrams of the advertisement calls of *B. mossambicus* from Mozambique Island, Lumbo and Nampula, Mozambique.

Specimens were weighed on a Sartorius PT120 portable balance accurate to 0.01 g, photographed using colour print film, and measured with vernier calipers accurate to 0.1 mm. They were preserved in 70 % ethanol and deposited in the collections of the Transvaal Museum, Pretoria (TM 70411–70498).

The description of morphology is restricted to those characters which have been mentioned in relatively recent publications, particularly those considered to have diagnostic value (e.g. Poynton 1964 1966 1982; Stewart 1967; Poynton & Broadley 1985; Lambiris 1989).

Recordings were made on standard magnetic tape cassettes using a Sony TCD5 PRO2 tape recorder and a Sennheiser ME80 microphone placed at a distance of 10–30 cm from the calling males. Three call bouts were recorded before each specimen was collected. A BAT12 digital thermometer was used to measure air and cloacal temperatures.

Narrow (45 Hz) and wideband (300 Hz) sonagrams of at least three advertisement calls of each specimen were produced using a KAY 7029A sound spectrum analyser. Bout and call variables measured are listed below. Statistical analysis of the data was performed using Statgraphics version 3.1. Pearson's correlation coefficients were calculated, and certain call variables influenced by temperature or body mass were adjusted using the slope of the regression line as a correction factor. Data were adjusted to a common air temperature rather than cloacal temperature, so that they could be more accurately compared with data from a previous study of *B. adspersus* in which air temperature was used (Minter 1995: 37–38).

Bout variables

- Bout duration(s): from the beginning of the first to the end of the last call.
- Number of calls: within a single call bout.
- Call rate (min^{-1}).
- Percentage grouped calls: number of grouped calls as a percentage of the total number of calls in a bout.
- Interval between calls: between two single calls; between a single call and a call group; between two call groups; between two calls within a call group.

Call variables

- Call duration(s): from the beginning of the first to the end of the last recognisable pulse, or, in non-pulsatile calls, the entire call.
- Number of pulses: within a single call.
- Pulse rate (s^{-1}): the time between the beginning of the first and the beginning of the last recognisable pulse divided by the number of pulses between these points.
- Dominant frequency (Hz): measured at the centre of the darkest band of the narrowband sonagram.

ADVERTISEMENT CALL STRUCTURE

B. mossambicus

The advertisement call data from the mainland populations sampled at Nampula (N = 20) and Lumbo (N = 5) are combined because they cannot be distinguished from one another morphologically, or by the mean or range of any call variables measured.

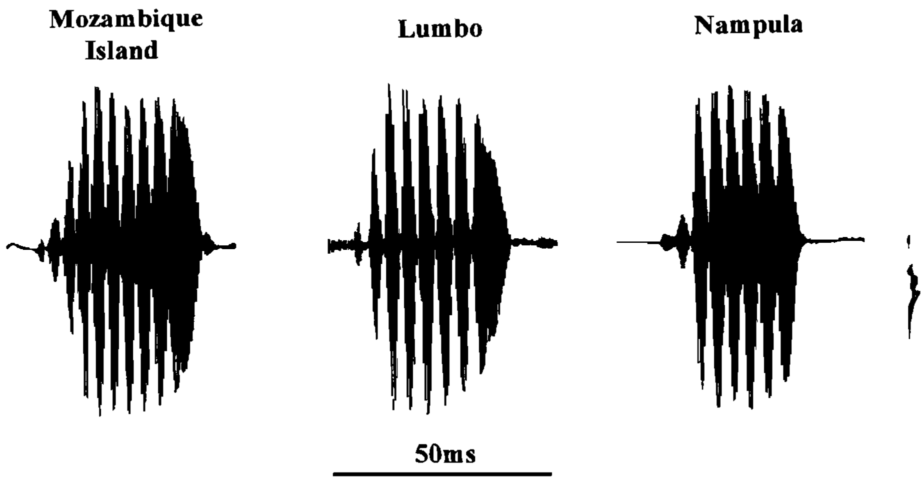

Fig. 2. Oscillograms of the advertisement calls of *B. mossambicus* from Mozambique Island, Lumbo and Nampula, Mozambique.

Structure and variation of call bouts

Island sample (Table 1):

The call bout lasts for up to 30 seconds and consists of 9–39 calls emitted at the mean rate of 106 calls per minute. On average, only 17 % of the calls are grouped: in a sample of 68 bouts from 58 different males, 83 % of the calls are single, 16 % are in groups of two and 1 % form groups of three calls. The interval between two calls within a call group is considerably shorter than the interval between two single calls, two call groups or a single call and a call group.

TABLE 1

Means and variability of call bout and advertisement call characters of *B. mossambicus* from Mozambique Island. Air temperature: range 24.8–27.9°C; mean 26.9°C; median 27.1°C; N = 58. Body mass: range 5.77–11.49 g; mean 8.63 g; median 8.71 g; N = 53.

Variable	N	Mean	SD	95 % confidence interval	Range	Coefficient of variation
Bout duration(s)	68	11.6	5.3	1.3	3.7–29.4	45.87
Number of calls	68	19	6.8	1.6	9–39	36.18
Call rate (min^{-1})	68	106	30.4	7.2	55–195	28.87
% grouped calls	68	17	25.3	5.9	0–96	149.36
Call interval(s):						
single-single	54	0.699	0.179	0.047	0.396–1.17	25.53
single-group	14	0.537	0.092	0.047	0.41–0.72	17.07
group-group	5	0.459	0.03	0.026	0.418–0.49	6.49
within-group	13	0.269	0.065	0.035	0.202–0.405	23.04
Call duration(s)	58	0.05	0.007	0.002	0.036–0.079	14.77
Number of pulses	58	10	1.2	0.3	7–13	12.94
Pulse rate (s^{-1})	55	192	14.8	3.9	152–229	7.71
Dominant frequency (Hz)	58	1792	80	21	1600–1937	4.49

The data do not yield significant correlations between temperature and call bout variables. This is possibly due to the narrow temperature range over which the calls were collected. No significant correlation was found between body mass and any call bout variable.

Mainland sample (Table 2):

Although the mean values for bout duration, number of calls and percentage of grouped calls differ in varying degrees from those of the Island sample, the ranges of these variables overlap entirely. Also, these variables have a high coefficient of variation, suggesting that they are not likely to be important in mate recognition.
The difference between the two samples with regard to the mean call rate can be attributed to the difference in mean temperature. It has been shown that in *adspersus*, call rate and air temperature are positively correlated (r = 0.64: Minter 1995, Table 2). Assuming that the same holds for *mossambicus*, then correction of the mean air temperature of the mainland sample (23.3°C) to that of the Island sample (26.9°C) would be accompanied by an increase in the mean call rate of the mainland sample (87 min^{-1}) bringing it closer to that of the Island population (106 min^{-1}). The same principle applies to call interval, which is negatively correlated with air temperature; as the temperature rises the call interval will decrease, reducing the differences between the two samples.

Structure and variation of individual calls

Island sample (Table 1; Figs 1 & 2):

The call consists of a very short pulsatile chirp which has a rapid rise and fall time. At about 27°C a typical call has a duration of 0.05 seconds and consists of about 10 pulses produced at a rate of 192 pulses per second. The pulses are equally spaced throughout the call, except at the end, where the last two or three pulses are closer together. A slight rise and/or fall in frequency is present in the calls of most specimens but no consistent, significant degree of frequency modulation was observed. An harmonic series is present, and the fundamental frequency is dominant (mean = 1792 Hz). The call and its harmonics have as many as three discrete sidebands on either side of the central, dominant frequency band (Fig. 1, NB).

Mainland sample (Table 2; Figs 1 & 2):

Because the data do not yield strong correlations between temporal call variables and air temperature, it was not possible to apply a temperature correction factor to the data. However, the difference in mean air temperature is relatively small (3.6°C) and, in the case of mean pulse rate which shows a positive correlation of r = 0.84 in *adspersus* (Minter 1995), correction of the data would merely reduce the difference between the samples. The means and ranges in call duration and in the number of pulses in the two samples, are very similar. Dominant frequency is negatively correlated with body mass (r = – 0.63 in *adspersus*), and correction of the heavier Island sample to the mean of the relatively lighter mainland sample would reduce the difference between the samples with regard to dominant frequency. The call characters all exhibit a low coefficient of variation; ie. they are relatively stable and are therefore more likely to be involved in mate recognition than the call bout characters.

TABLE 2

Means and variability of call bout and advertisement call characters of mainland *B. mossambicus* populations from Nampula and Lumbo, combined. Air temperature: range 22.5–24.8°C; mean 23.3°C; N = 25. Body mass: range 1.73–7.78 g; mean, 4.68 g; N = 24.

Variable	N	Mean	SD	95 % confidence interval	Range	Coefficient of variation
Bout duration(s)	33	15.2	5.4	1.8	5.5–24.8	35.52
Number of calls	33	22	8.3	2.8	8–41	37.65
Call rate (min^{-1})	33	87	9.9	3.4	69–103	11.4
% grouped calls	33	7	12.7	4.3	0–44	180.15
Call interval(s):						
single-single	24	0.734	0.143	0.057	0.467–1.1	19.49
within group	2	0.273	0.033	0.045	0.250–0.296	11.92
Call duration(s)	25	0.051	0.006	0.003	0.04–0.065	12.35
Number of pulses	25	9	0.9	0.4	7–11	10.49
Pulse rate (s^{-1})	25	174	8.9	3.5	160–198	5.08
Dominant frequency (Hz)	25	1935	96	38	1780–2193	4.94

Comparison of Island sample of *B. mossambicus* with *B. adspersus* from Pietersburg

In order to compare the advertisement calls of these species, the relevant call variables of the Pietersburg sample of *B.adspersus* (Minter 1995, Table 1) were corrected to the median air temperature and body mass of the Island sample of *B. mossambicus*. However, since the ranges in air temperature of the two samples do not overlap (9.5–20.3°C in *adspersus*, 24.8–27.9°C in *mossambicus*), the corrected temporal variables should be treated with circumspection. This is because correction of the data requires extrapolation beyond the limits of the temperature range of the *adspersus* sample and assumes that the correlation between the variables (i.e. the slope of the regression line) does not change beyond these limits. This problem does not arise in the case of the spectral variable, dominant frequency, because the ranges in body mass of the two samples overlap broadly (3.56–9.53 g in *adspersus*, 5.77–11.49 g in *mossambicus*).

Characters which do not require correction because they are not correlated with temperature or mass, are the percentage of grouped calls and the number of pulses in the call.

With regard to call bout characters, correction of the call interval within call groups in the *adspersus* sample results in a fairly close correspondence between the two species in respect of this character (corrected *adspersus* mean 0.2 s; range 0.034–0.381 s). The percentage of grouped calls and the number of calls within call groups in *mossambicus* are considerably lower than in *adspersus*, in which 83 % of the calls are grouped and 43 % are emitted in groups of three or more (Minter 1995, Fig. 2).

Correction of the mean call duration of *adspersus* reduces it from 0.207 s to 0.096 s, which is still roughly twice the mean call duration of *mossambicus*. However the range in corrected call duration of *adspersus* (0.037–0.163 s) broadly overlaps that of the *mossambicus* sample. Correction of the *adspersus* pulse rate data (mean 190 s^{-1}; range 153–215 s^{-1}) results in a very close correspondence between the *adspersus* and

mossambicus samples. *B. adspersus* calls contain more pulses (mean 24; range 17–31) than the *mossambicus* calls and their ranges in respect of this call character do not overlap. The corrected dominant frequency of the *adspersus* calls (mean 1655 Hz; range 1516–1801 Hz) does not differ significantly from that of the *mossambicus* sample.

TABLE 3

Means and variability of call bout and advertisement call characters of the combined Island and mainland populations of *B. mossambicus*. Air temperature: range 22.5–27.9°C; mean 25.8°C; N = 83. Body mass: range 1.73–11.46 g; mean, 7.4 g; N = 77.

Variable	N	Mean	SD	95 % confidence interval	Range	Coefficient of variation
Bout duration(s)	101	12.8	5.6	1.1	3.7–29.4	43.78
Number of calls	101	20	7.5	1.5	8–41	37.45
Call rate (min^{-1})	101	100	26.9	5.3	55–195	27.06
% grouped calls	101	14	22.4	4.4	0–96	163.52
Call interval(s):						
single-single	78	0.71	0.168	0.037	0.395–1.17	23.69
single-group	14	0.537	0.092	0.047	0.41–0.72	17.07
group-group	6	0.452	0.03	0.026	0.415–0.49	7.15
within group	15	0.269	0.061	0.031	0.202–0.405	22.44
Call duration(s)	83	0.05	0.007	0.001	0.036–0.079	14.08
Number of pulses	83	9	1.2	0.3	7–13	12.3
Pulse rate (s^{-1})	80	187	15.6	3.4	152–229	8.34
Dominant frequency (Hz)	83	1835	107	23	1600–2193	5.84

B. poweri

(Table 4, Figs 3–5)

Structure and variation of call bouts

In a sample of 47 call bouts from 40 males, the bout lasted for up to 30 seconds and consisted of 10–74 calls emitted at a mean rate of 175 calls per minute. Most (99.6 %) of the calls were grouped; 43 % formed groups of 4–5 calls, while 39 % formed larger groups of up to 17 calls.

The interval between two calls within a call group was considerably shorter than the interval between two call groups (Fig. 3). The calls are closer together within the group (0.235 s) than in *adspersus* (0.54 s), but this may be due to the higher mean air temperature of the Island sample (26.9°C cf. 15.7°C in the *adspersus* sample), since a negative correlation exists between call interval and air temperature (Minter 1995, Table 2).

Structure and variation of individual calls

The call is a short whistle with a mean duration of 0.14 seconds, and a slow rise and rapid fall time (Fig. 4). An harmonic series is present, and the fundamental frequency is dominant (mean = 1728 Hz). Frequency modulation occurs in the form of a slight rise in frequency towards the end of the call. The oscillogram (Fig. 5) is

puzzling since it seems to reveal masked amplitude modulation within the call. However, these 'masked pulses' do not generate sidebands in the narrow band sonagram (Fig. 3, NB), and it is unlikely that they are perceived by the female. Nevertheless it is interesting to note that there are as many 'masked pulses' in the call of *B. poweri* as there are pulses in the call of *B. adspersus*. Dominant frequency, call duration and the call interval within groups all exhibit a low coefficient of variation, i.e. they are highly stable call characters. The data do not yield significant correlations between temporal call variables and air temperature, possibly because of the narrow temperature range over which the calls were recorded. The correlation between body mass and dominant frequency was relatively low ($r = -0.52$, $p = .001$, $N = 39$).

TABLE 4

Means and variability of call bout and advertisement call characters of *B. poweri from Nampula.*
Air temperature: range 22.3–23.8°C; mean 25.5°C; N = 40.
Body mass: range 4.04–10.28 g; mean: 6.9 g; N = 40.

Variable	N	Mean	SD	95 % confidence interval	Range	Coefficient of variation
Bout duration(s)	47	8.2	6.1	1.8	3.0–29.7	58.85
Number of calls	47	30	16.3	4.7	10–74	54.89
Call rate (min^{-1})	47	175	27	8	124–251	15.17
% grouped calls	47	99.6	1.26	0.36	94–100	1.27
Call interval(s):						
group-group	35	0.743	0.166	0.055	0.5–1.1	22.37
within group	40	0.235	0.02	0.006	0.176–0.26	8.38
Call duration(s)	40	0.140	0.012	0.004	0.111–0.16	8.89
Dominant frequency (Hz)	40	1728	83	26	1557–1903	4.77

These advertisement calls are similar to those recorded at Solwezi, Zambia, by Prof. A. Channing (sonagram examined). The latter locality is 350 km NW of the type locality of *B. poweri* (Kabwe, Zambia) and 1450 km WNW of Nampula.

MORPHOLOGY

B. mossambicus

Physical dimensions

Island sample: male SVL: mean 37 mm; range 30.8–40.3 mm; N = 17.
female SVL: mean 50.8 mm; range 49–53.4 mm; N = 3.
male body mass: mean 8.63 g; range 5.77–11.49 g; N = 53.
female body mass: mean 26.8 g; range 23.9–27.9 g; N = 3.

Mainland sample: male SVL: mean 30.2 mm; range 21–34.4 mm; N = 24.
male body mass: mean 4.68 g; range 1.73–7.78 g; N = 24.

Combined sample: male SVL: mean 33 mm; range 21–40.3 mm; N = 41.
male body mass: mean 7.4 g; range 1.73–11.46 g; N = 77.

Dorsal and lateral colour and markings

Island sample (N = 20):

All specimens uniform light brown, with conspicuous black spots (illustrated in Poynton & Broadley 1985: 519) that vary considerably in number and size; some individuals almost immaculate while others, especially females, are heavily spotted and even blotched. Three individuals possess a few small, inconspicuous red patches. Fine, light lateral speckling present in all specimens, but is usually inconspicuous. An interocular bar is present but very indistinct in 13 specimens and absent in seven. Paravertebral patches entirely absent, as are dorsolateral patches, except for one individual which exhibits indistinct patches on one side of its body. A narrow, light vertebral line extends forward to reach head in two specimens, is shorter and sometimes indistinct in 16 and absent in two. A light line running from heel-to-heel is present in all specimens but indistinct in 11. An oblique dark stripe runs from the eye downwards and backwards to base of arm and, with only one exception, is separated from the dark gular patch by a light stripe extending from upper jaw to arm; in one specimen the dark stripe joins the gular patch.

Mainland sample (N = 26):

Most (24) specimens dark brown to black, while two from Lumbo are light brown. Indistinct dark spots scattered over the entire dorsum are present in 14 specimens, while in 12 the background colour is so dark that the spots, if present, are not discernible. A red or pink suffusion is visible in 21 specimens, spread across entire dorsum except in darker specimens where it is only visible laterally or is restricted to the light area behind the eyestripe. Five specimens show no red colouring. Fine, light lateral speckling present but usually indistinct in 13 specimens, and absent in 13. An interocular bar is barely discernable in 14 specimens and absent in 12. Paravertebral and dorsolateral patches absent in all individuals, except two which have indistinct dorsolateral patches on one side of body. A narrow, light vertebral line present in seven specimens and absent in 19; where present it is usually short and indistinct. A light line running from heel-to-heel is distinct in two specimens, indistinct in nine and absent in 15. An oblique dark stripe runs from eye downwards and backwards to base of the arm and joins dark gular patch in 18 specimens, while in four it is separated from gular patch by a light stripe extending from upper jaw to arm; four specimens show a combination of these two character states.

Ventral colour and markings

Island sample:

Gular region uniformly dark anteriorly and freckled posteriorly in 13 specimens, while in seven specimens entire gular region is freckled. Pectoral and abdominal regions are immaculate in all specimens.

Mainland sample:

Entire gular region uniformly dark in all specimens. Pectoral region uniformly darkened in two individuals, freckled in 21 and immaculate in three. Abdomen is immaculate in all but two specimens which are slightly freckled.

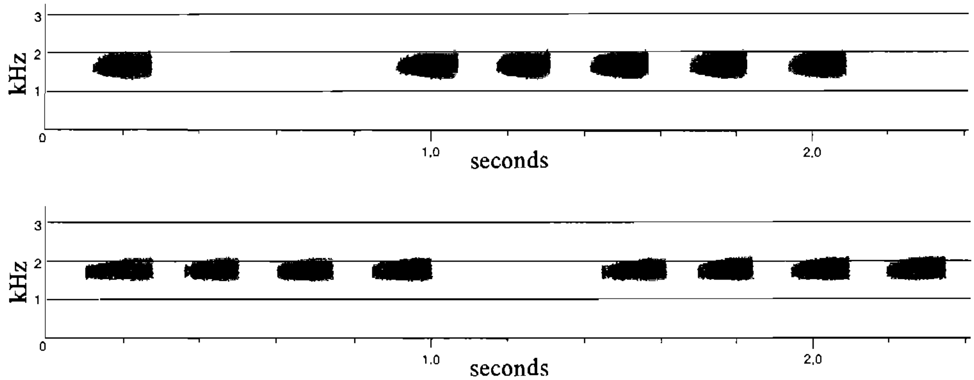

Fig. 3. Grouping of calls within the call bout of *B. poweri* from Nampula, Mozambique.

Hands and feet

Island sample:

Outer finger in all specimens falls just short of distal subarticular tubercle of fourth finger. Subarticular tubercles of fourth finger undivided in all specimens. Inner and outer metatarsal tubercles separated by deep cleft in 16 specimens, and a shallow groove in four. Outer toe in all specimens reduced to a stub which falls short of basal subarticular tubercle of fourth toe.

Mainland sample:

Outer finger in all specimens falls just short of distal subarticular tubercle of fourth finger. Subarticular tubercles of fourth finger undivided in all specimens except two, each of which have divided tubercles on one hand only. Inner and outer metatarsal tubercles separated by a deep cleft in 14 specimens, a shallow groove in nine, and are fused in three individuals. Outer toe in all specimens reduced to a stub which falls short of basal subarticular tubercle of fourth toe.

B. poweri (N = 41)

Physical dimensions

Male SVL: mean 35.5 mm; range 30.4–39.3 mm; N = 39.
Male body mass: mean 6.9 g; range 4.04–10.28g; N = 40.
Female SVL: 53 mm; N = 1.
Female body mass: 20.9 g; N = 1.

Dorsal and lateral colour and markings

Most (32) specimens are dark brown with numerous indistinct, very dark spots scattered over entire dorsum, resulting in a mottled appearance; in nine specimens the background colour is so dark that the spots are scarcely discernible and specimens appear uniformly coloured rather than mottled. Eight specimens are light brown with more clearly defined dark spots. One specimen also shows a few small red patches on dorsum. An interocular bar is well defined in two specimens, indistinct in 37, and absent in two. Paravertebral patches relatively well defined in one specimen, present

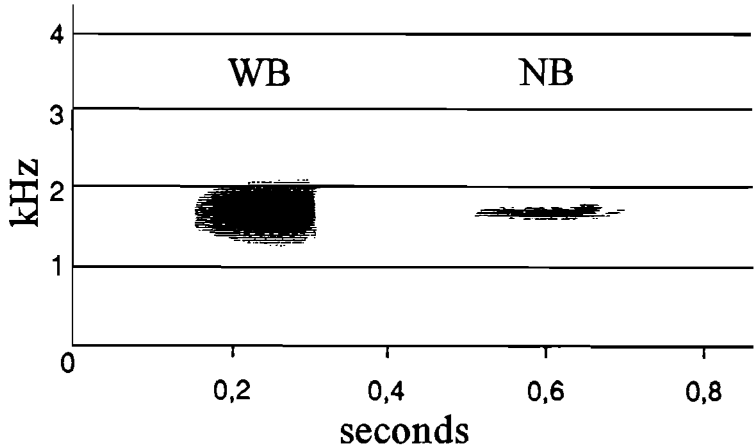

Fig. 4. Wide (WB) and narrow band (NB) sonagrams of the advertisement call of *B. poweri* from Nampula, Mozambique.

but indistinct in 39 and absent in one. Well-defined bright yellow or cream dorsolateral patches present in 40 individuals, but indistinct in one very dark specimen. A narrow, light vertebral line extends forward to reach head in 31 specimens but is shorter in nine and absent in one. A light line running from heel-to-heel is present in 40 and absent in one individual. At intersection of vertebral and heel-to-heel lines, a light patch is clearly developed in 13 specimens, indistinct in 21 and absent in seven. An oblique dark stripe runs from eye downwards and backwards and, in 15 specimens, curves forwards to join dark gular patch; in 16 individuals it ends at base of arm and is separated from gular patch by a light stripe extending from upper jaw to arm. This stripe is broad in the female speciman and relatively narrow in males. Seven specimens show combination of preceding two character states.

Ventral colour and markings

Gular region uniformly dark brown to black in all male specimens and mottled in the female. Pectoral region freckled in all specimens and abdomen immaculate in all but one, which is slightly freckled.

Hands and feet

In all specimens, outer finger reaches or barely reaches proximal subarticular tubercle of fourth finger and never extends beyond it. Subarticular tubercles of fourth finger undivided in all specimens except one, which has a divided tubercle on one hand only. Inner and outer metatarsal tubercles separated by a deep cleft in two specimens, a shallow groove in 12 and are completely fused in 27. Outer toe in all specimens reduced to a stub which falls short, to well short of basal subarticular tubercle of fourth toe.

FIELD NOTES

B. mossambicus

Mozambique Island is approximately 3 km long and 800 m wide and is connected to the mainland by a bridge 3.5 km long. Although the Island now has a large human

population and little unoccupied space remains, an emergence of large numbers of these frogs, as described by Peters (1882: 117): 'während des Regens in ungeheurer Zahl aus der Erde hervorkam', was observed in the public park adjacent to the Fortress at the northern end of the island, before dawn on 5th December, following heavy rain. As many as 12 frogs per m^2 were seen on the surface at first light; groups of 2–4 individuals were observed feeding on worker termites at emergence holes in the soil, while others moved about at random on the surface. No calling was heard at this time, but a strong chorus developed in the evening.

On the evenings of the 30/11–3/12 intermittent, light showers fell and some weak calling was heard but a chorus did not develop. There was, however, a lot of surface activity involving aggressive interactions between males. Two males were observed standing upright whilst pushing against each another with their upper bodies and their arms. The opponents circled each other, locked in combat, until one broke away and moved off. A calling male was observed to increase its call rate and turn to face an approaching male which advanced to within 5 cm and then moved away without making contact.

Most males (62) called from exposed positions on the surface, while others (20) occupied shallow depressions similar to those constructed by *B. adspersus* (Minter 1995). Call sites were sometimes concealed beneath vegetation or leaf-litter. Calling usually commenced after dark but some Island males were heard calling during the day in light rain.

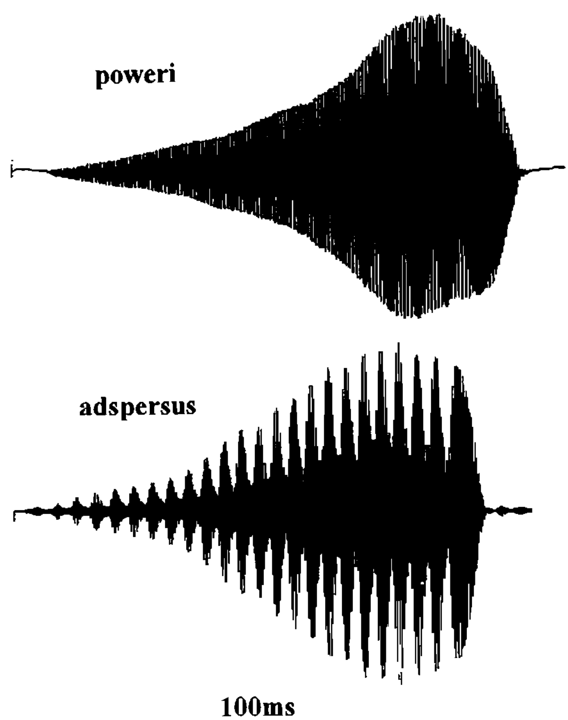

Fig. 5. Oscillograms of the advertisement calls of *B. poweri* from Nampula, Mozambique, and *B. adspersus* from Pietersburg, South Africa.

B. poweri

At Nampula a strong *poweri* chorus developed before sunset on both days, whereas *mossambicus* only began calling after dark. Most (38) males were calling from the surface, while 3 were calling from shallow depressions, partly concealed by vegetation or leaf-litter. Calling continued until just before dawn. Amplexus is accompanied by the production of a sticky secretion, as in *adspersus*.

DISCUSSION

Advertisement calls

No significant difference was found between the Island and mainland samples of *B. mossambicus* with regard to call bout or advertisement call variables. These data are therefore combined in Table 3, to create a larger, more representative data set for *B. mossambicus*. Call duration, number of pulses, pulse rate and dominant frequency exhibit relatively little variation within or between the populations sampled. The stability of these characters enhances their potential diagnostic value and also suggests that they are involved in mate recognition.

The advertisement calls and call bouts of the Island population of *mossambicus* differ from those of the Pietersburg population of *adspersus* in that the calls are shorter and consist of fewer pulses. A smaller percentage of the calls are grouped and the call groups themselves are smaller. The latter two characters are most useful when comparing choruses of moderate to high intensity. The distinction becomes less obvious as the chorus intensity drops, because *adspersus* then tends to reduce the size of the call groups and gives a higher percentage of single calls.

The advertisement calls of *B. poweri* are easy to distinguish from those of *mossambicus*; they are non-pulsatile, of longer duration and form very large groups within the call bout. No evidence of hybridisation was observed at Nampula where the two species were calling side by side. The main difference between *poweri* and *adspersus* calls is that the former are non-pulsatile; a higher percentage of *poweri* calls are grouped and the groups themselves are much larger than in *adspersus*.

Morphology

The *mossambicus* specimens examined in this study closely match the description by Poynton & Broadley (1985). The only additional variation that may be noteworthy, is that the inner and outer metatarsal tubercles are fused in a few (3) mainland specimens. The fact that most mainland specimens are much darker dorsally than those from Mozambique Island can be attributed to crypsis and the fact that the Island has a light brown sandy soil, while the substrate at mainland localities is a grey loamy soil. The mainland specimens are smaller, on average, than the Island population, but the ranges in SVL and body mass overlap considerably. The absence of paravertebral and dorsolateral patches, and the relatively longer outer finger distinguish *mossambicus* from *poweri* in this area.

The *poweri* sample differs morphologically from the material examined by Poynton & Broadley (1985) in the following ways: the light patch at the intersection of the vertebral and heel-to-heel lines is a very variable character and is indistinct or

absent in a number of specimens; the dark infraorbital stripe is not always separated from the dark gular patch by a broad light band from upper jaw to arm, but is continuous with the gular patch in a number of specimens. Also, the light band is usually narrow in males. This variation diminishes the diagnostic value of these characters.

General remarks

These data may be used to test the hypothesis that hybridisation occurs between *adspersus* & *mossambicus* by analysing advertisement calls from areas of sympatry. The relationship between *poweri* and *adspersus* also invites investigation. A study of the functional morphology of the larynx of these two species might show why *adspersus* produces a pulsatile call and *poweri* a non-pulsatile call, and explain the apparent presence of masked pulses in the *poweri* call.

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